

A REVISION OF THE ANT GENUS POLYRHACHIS
AT THE SUBGENERIC LEVEL
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Polyrhachis is a large genus containing about 500 nominal forms. Although it is mostly confined to the tropics and subtropics of the Old World, there are two species found in Japan, one species in Korea, and several species in Central China. None has been found in Madagascar and the neighboring islands, or on New Zealand and the Pacific islands east of the New Hebrides. Ants of this genus are characterized by monomorphism and by the alitrunk and petiole usually being armed with spines or teeth, whence the name *Polyrhachis*.

To date, 19 subgenera have been recognized in this genus: *Anoplomyrma*, *Aulacomyrma*, *Campomyrma*, *Cephalomyrma*, *Chariomyrma*, *Cyrtomyrma*, *Dolichorhachis*, *Evelyna*, *Florencea*, *Hagiomyrma*, *Hedomyrma*, *Johnia*, *Morleyidris*, *Myrma*, *Myrmatopa*, *Myrmotherinx*, *Myrmhopla*, *Polyrhachis*, and *Pseudocyrtomyrma*. Among these, only *Myrma* and *Pseudocyrtomyrma* are known to occur in Africa. The 19 subgenera were proposed mostly on the basis of peculiarities in the structure of the alitrunk and petiole. But in most cases they are not well-defined. Some subgenera may seem quite distinct from others occurring in the same general area. But they are not delimitable when specimens from all over the whole range of this genus are brought together. The status of the subgenera will be discussed in the following sections.

METHODS AND CHARACTERS STUDIED

This study is based mainly upon the same external morphological characters of workers traditionally used in the taxonomy

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of this group. The structure of alitrunk and petiole afford basic diagnostic characters in most groups. Besides the gross external morphological characters of workers, some other characters were also studied: proventriculus of worker, wing venation, and genitalia of male. But they proved to be quite similar throughout the genus. In addition to the morphological characters mentioned above, the nesting behavior and geographic distribution were considered, mostly from literature sources.

THE VALIDITY OF THE GENERIC NAME POLYRHACHIS

The name *Polyrhachis* was first suggested by Shuckard in 1840 as the generic name of a group of ants that he recognized to be a distinct group. But he did not live to give a description of this genus, or to cite any species belonging to it. Therefore the name was a *nomen nudum*. It was in 1857 that Frederick Smith described some twenty species of *Polyrhachis* and designated *Formica bihamata* as the type (Smith 1857, p. 58). Gerstäcker also described an African ant, *Hoplomyrmus schistaceus* (Gerstäcker 1858, p. 262) which is clearly congeneric with the forms included by Smith in *Polyrhachis*. Since Gerstäcker's paper was published one year later, *Hoplomyrmus* is certainly junior to *Polyrhachis*. However, in 1820, Billberg had already in his "Enumeratio Insectorum" established this group of ants under another name. On p. 104 of this obscure work, we find the following:

G. Myrma Eg. — Formica ol.

Carinata N. Chalced. Fbr. Hystrix Eg. 2.

militaris Afr. aequin. —

The "Eg." in this citation stands for Billberg. Both *carinata* and *militaris* cited here by Billberg have long been recognized as *bona fide* members of the genus *Polyrhachis*. Since *hystrix* is a *nomen nudum*, Wheeler in 1911 designated *militaris*, one of the two other species cited in Billberg's original paper, as the type of the genus *Myrma*, and claimed that both *Polyrhachis* and *Hoplomyrmus* are junior synonyms of *Myrma*.

If we trace Wheeler's papers from 1911 down to 1915, we will find that in 1912 he still used the name *Myrma* and subordinated *Polyrhachis* as a subgeneric name, and cited *sexspinosa* as

a "*Myrma* (*Polyrhachis*)" though it actually belongs to the subgenus *Myrmhopla*. He still did not make any correction in his paper in 1913, and nothing on this group of ants was published by him in 1914. But suddenly in 1915 he began to use *Polyrhachis* instead of *Myrma* (Wheeler 1915a), and no reason was given for his change of mind. All we know is that Emery, Santschi and Forel strongly objected to Wheeler's proposal to substitute *Myrma* for *Polyrhachis* (Forel 1915b). This may have influenced him. Since then, *Polyrhachis* has been used for the genus in all works known to me.

According to the International Code, Article 23, *Myrma* could be considered as a valid name. But in item (b) of the same article, it says: "A name that has remained unused as a senior synonym in the primary zoological literature for more than fifty years is to be considered a forgotten name (*nomen oblitum*)."

Certainly, the name *Myrma* had only been used by Wheeler as a generic name for three years, and more than 50 years ago. However, we must not ignore the fact that it has not really been forgotten, but has been used as a subgeneric name instead. The important thing is that in item (c) of the same article, it also says: "The priority of the name of a taxon in the family-, genus-, or species-group is not affected by elevation or reduction in rank within the group." This certainly implies that although *Myrma* has been treated as a subgeneric taxon, it still has its priority over *Polyrhachis*. That is to say, *Myrma* is still the strictly valid generic name for this group of ants. Nevertheless, in this revision, the name *Polyrhachis* is retained, and this nomenclatural problem will be left to future revisers and the deliberations of the International Commission.

It is to be hoped that the familiar name of this important genus can be retained. *Polyrhachis* and *Myrma* are considered as subjective synonyms on the basis of evidence cited above. The replacement of the first name by the second would cause nomenclatorial chaos, not only for the 500 species directly involved, but also elsewhere in the classification of the family Formicidae. Already we have such genera (tribes, subfamilies) as *Myrmecia* (Myrmeciini, Myrmeciinae), *Myrmica* (Myrmicini, Myrmicinae),

Myrmecina (Myrmecini), and others with similar names involving the stem *Myrm*-, all in one family. The addition of a genus *Myrma* would only compound the confusion that already exists.

HISTORICAL SKETCH

This group of ants was first established obscurely by Billberg in 1820 under the generic name *Myrma* with two species, *carinata* and *militaris*. But another generic name, *Polyrhachis*, was introduced by Frederick Smith in 1858. The validity of these two generic names is discussed in the previous section. Under this genus Wheeler (1911) recognized five subgenera:

Campomyrma Wheeler (Type: *Polyrhachis clypeata*)

Myrma Billberg (type: *Formica militaris*)

Polyrhachis Fr. Smith (type: *Formica bihamata*)

Hagiomyrma Wheeler (type: *Formica ammon*)

Hemioptica Roger (type: *Hemioptica scissa*)

However, the subgenus *Hemioptica* was later elevated as a distinct genus by Emery in 1925 because of its unique alitrunk, which has a deep transverse furrow between mesonotum and propodeum.

Forel in 1915 included another six subgenera under *Polyrhachis*:

Chariomyrma Forel (type: *Polyrhachis guerini*)

Cyrtomyrma Forel (type: *Formica rastellata*)

Hedomyrma Forel (type: *Polyrhachis ornata*)

Myrmatopa Forel (type: *Polyrhachis schang*)

Myrmhopla Forel (type: *Formica armata*)

Myrmothrinax Forel (type: *Polyrhachis thrinax*)

In 1919, Mann erected subgenus *Dolichorhachis*, with type species *malaënsis*, which he himself described from the Solomon Islands. Subgenera *Aulacomyrma* and *Pseudocyrtomyrma* were both erected by Emery in 1921, with type species *Polyrhachis porcata* and *P. revoili* respectively. *Polyrhachis (Johnia) schizospina* was described by Karawajew in 1927 as a new species and subgenus. He also described another species *Polyrhachis (Cephalomyrma) stylifera* in 1935 as *sp. et subgen. nov.* Subgenus *Florencea*, with type species *kirkae*; and subgenus *Evelyna*, with type

species *cheesmanae*, were described in 1937 by Donisthorpe in two papers. In 1944, he created another subgenus *Morleyidris*, with type species *trina*, from New Guinea. Almost twenty years elapsed, when in 1963, Chapman described *Polyrhachis parabiatica* in his new subgenus *Anoplomyrma*. At present 19 subgenera are recognized in this genus. Their systematic validity will be discussed in this paper.

THE VARIABILITY OF THE PETIOLE IN POLYRHACHIS

In *Polyrhachis*, the shape of the petiole varies considerably among different subgenera, and even among consubgeneric species. In the subgenus *Polyrhachis*, there are only two spines on the petiole; these rise vertically and are either parallel for some distance, or diverge widely from their base (fig. 97), or are parallel for a part of their length and then diverge (fig. 95). In *Cyrtomyrma*, the petiole tends to be scale-like with four subequal acute teeth or spines, the median two close together and vertical. But there is a tendency for the lateral pair to elongate (figs. 89-93).

Among *Myrmhopla*, the form of the petiole varies according to groups. In the groups *cryptoceroides* and *dives*, there are two laterally spreading spines curved to the shape of the abdomen, and two or three medial short obtuse teeth. In groups *viehmeyeri*, *sexspinosa*, and *nigriceps*, the medial teeth are missing, and the two lateral spines are short, and may even be so rudimentary that they look like two denticles, as in *Polyrhachis nigriceps* (fig. 83). Most of the ants in group *armata* have the petiole without medial teeth, but with two moderately long lateral spines. But *furcata* has two long spines rising above, with their apical halves curved backward, downward, and slightly outward as in *lamellidens*.

In *Myrma*, the petiole is usually armed with two pairs of teeth, i.e., at its upper lateral angles it has two erect spines, and on each side beneath their bases there is a laterally directed, acute shorter spine (fig. 30). These four spines may sometimes be subequal (fig. 36). But the lateral spines are occasionally absent, as in *philippinensis* (fig. 45), or the medial spines may even be bent like hooks as in *laboriosa* (fig. 32). In *orsyllus*, the medial pair is reduced, and the upper edge of the scale is arched (fig. 46).

In some African species, for instance *decendentata* and *andrei*, an extra spine may be found under the lateral spines (fig. 47).

In *Campomyrma*, the petiole is ordinarily furnished with four spines of nearly equal distance from another (fig. 2). But the median pair may also reduce to be dentate as in *halidayi* (fig. 8), or may even be completely missing, as in *semipolita* (fig. 12). In some species, such as *clypeata* (fig. 2), the median pair is elongate, and finally, in some species, the lateral spines are wanting (fig. 5). *Polyrhachis schwiedlandi* has the petiole shaped as in *orsyllus*, and one species from Australia has a three-spined petiole (fig. 6).

The petiole in *Myrmotherinax* is less variable. There are three spines, with the medial one longer than the other two, and in some cases, the middle spine is bimucronate (fig. 19). However, in *unicuspis* (fig. 17), the lateral spines are missing and only the middle spine remains.

The above discussion leads to the conclusion that the petiole is so variable among consubgeneric species that it can not be used as a subgeneric character in *Polyrhachis*. Yet there are at least five monotypic subgenera that are recognized merely on the shape of the petiole.

In 1927, Karawajew described subgenus *Johnia*, with the type species *schizospina*, based on one female from Prince's Island, Sunda Strait. In his original description he mentioned that *Johnia* is closely related to *Aulacomyrma*, except for the shape of gaster and petiole (Karawajew 1927, p. 43). Actually, the gaster of *schizospina* as he described it is very much the same as in *P. (Aulacomyrma) mystica*. As for the petiole (fig. 80), it is usual among *Polyrhachis* that the females have this segment with spines absent or at least shorter than in the workers. It is obvious that the specimen Karawajew described is only a female of the subgenus *Aulacomyrma*. In 1935, he described another monotypic subgenus, *Cephalomyrma*, with the type species *stylifera*, based upon a single worker from the Gulf of Siam in Cambodia. As he described in his paper, this subgenus is closely related to *Myrmhopla*, with alitrunk rounded off. The main difference is the petiole with two lateral spines truncate, rather than pointed as in

Myrmhopla (figs. 81, 82).

Polyrhachis (*Evelyna*) *cheesmanae* was described in 1937 as *subgen. et sp. nov.* by Donisthorpe, based also on a single female specimen from Kokoda, Papua. In his original description, Donisthorpe (1937b, p. 273) states "This new subgenus comes very near to *Cyrtomyrma* Forel, from which it differs in having only three teeth on the scale instead of four." No doubt this is a *Myrmothrinax* female. Another interesting species, *P. (Florencea) kirkae* (fig. 101), was also described by Donisthorpe from Kokoda, Papua, in 1937. This form mimics the myrmicine ant *Aphaenogaster loriai*. He claimed in his original description that "This new subgenus comes near to W. M. Mann's *Dolichorhachis* (misspelling of *Dolichorhachis*) in some respects, but the absence of any margins to the thorax and especially the want of spines to the petiole renders it abundantly distinct. The latter character and the epinotal structure also separate it from the subgenus *Myrmhopla*." (Donisthorpe 1937a, p. 625). At first sight, "the want of spines to the petiole" sounds like a good subgeneric character. But if we study some other species from New Guinea, we will find that some *Myrmhopla* also have a petiole with obsolete spines; typical examples are species of the *nigriceps* group (fig. 83), in which *kirkae* clearly belongs. In fact, even the specific distinctness of *kirkae* and *nigriceps* is doubtful. Subgenus *Morleyidris* was described in 1944 by Donisthorpe, for the monotypic species *trina* from Mt. Cyclops, Dutch New Guinea, also based on a single worker. The specimen he used for his description is not available for this study, but his original description will be quoted here. On page 64, he said "This new subgenus comes nearest to *Hedomyrma* Forel and agrees with most of the characters of that subgenus of *Polyrhachis* Fr. Smith; but the petiole is quite different in shape, being rounded at the base and armed with two circular curved spines." (Donisthorpe 1944) (figs. 66, 67). As I have already said, the shape of the petiole varies so much, not only among different subgenera but also among consubgeneric species, that it is not advisable to use it as a subgeneric character. If we want to recognize *Morleyidris* as a distinct subgenus differing from *Hedomyrma* merely in the shape of the petiole, then we should also have to raise such variant forms as *furcata*, *laboriosa*,

and *unicuspis* as monotypic subgenera. This kind of subdivision is certainly too artificial.

On the evidence given above, five subgenera of the genus *Polyrhachis* can be synonymized summarily as follows:

Aulacomyrma Emery 1921 = *Johnia* Karawajew 1927. *Syn. nov.*

Hedomyrma Forel 1915 = *Morleyidris* Donisthorpe 1944. *Syn. nov.*

Myrmhopla Forel 1915 = *Cephalomyrma* Karawajew 1935. *Syn. nov.* = *Florencea* Donisthorpe 1937. *Syn. nov.*

Myrmothrinax Forel 1915 = *Evelyna* Donisthorpe 1937. *Syn. nov.*

INTEGRATION OF THE SUBGENERA IN POLYRHACHIS

If we assume that subgenus *Campomyrma* represents the primitive stock in this genus, we find that the other subgenera can be derived directly or indirectly from this subgenus, so far as the morphological characters are concerned. However, the subgeneric divergence is not great, at least in most cases. The subgenera are still so well connected with each other by intermediate forms that a clear-cut delimitation is impossible (except the subgenus *Polyrhachis*, which will be discussed in detail).

In *Campomyrma* (figs. 1-14), the alitrunk is margined along the sides; pronotum laminated or dentate; propodeum projects behind in one pair of lamellar appendages or spines, sometimes reduced to short teeth or tubercles. Promesonotal suture is always distinct, while a mesonotal groove is well-defined only in a few Australian species and most Philippine ones. In some species, such as *P. clypeata*, *P. halidayi*, and *P. hauxwelli*, this groove is replaced by a ridge. It is represented only by a fine suture in the rest of this subgenus. The propodeum is sometimes much longer than broad, as in *P. prometheus* (fig. 5). The petiole varies even more than the alitrunk. It has four, three, or two spines, or may only have a scale-like node, as seen in *P. schwiedlandi* (figs. 2, 4, 5, 6).

The subgenus *Myrmothrinax* (figs. 15-19) shares most characters with *Campomyrma*, except that the petiole has three spines.

Yet this character is not unique at all, as in *Campomyrma*, one species from Australia (fig. 6) has only three spines on the petiole too! Besides, *P. (Myrmatopa) solivaga* also has a small tooth between the two lateral spines (fig. 21); further, some *Myrmotherinx* have the median tooth divided into two.

The *schang* group of the subgenus *Myrmatopa* looks at first sight like a distinct unit by itself, because of the rounded pronotum and mesonotum with raised angular sides. But this morphological extreme is connected with *Campomyrma* by the *wallacei* group of the same subgenus. For example, in *P. edwardi* (fig. 26) and *P. fruhstorferi*, the alitrunk is margined all along the sides, and the pronotum is dentate. The pronotal margin gradually disappears, as seen in a morphocline through the *wallacei* group (fig. 22). The only difference between the *wallacei* group of the subgenus *Myrmatopa* and the subgenus *Campomyrma* is that the former has the petiole with two spines. But this is also found in some *Campomyrma*, such as *P. semipolita*.

The subgenus *Myrma* (figs. 29-47) has the widest geographical distribution in this genus. It occurs in both Africa and Asia. In this subgenus, the alitrunk is margined. Pronotum prolonged forward as two straight spines, parallel or divergent. Propodeum unarmed or armed with teeth or small spines, ordinarily erect. Promesonotal suture distinct. But metanotal groove distinct only in some African species (figs. 29, 31, 34, 35). Petiole with spines varying from one to three pairs, or even simply scale-like. Although this subgenus is well characterized in some species, still there are species that appear to be closely related to *Campomyrma*. One species from Pretoria, South Africa, found in Dr. Creighton's collection, has the alitrunk shaped decidedly as in *Campomyrma* (figs. 38, 39). Its petiole may serve to indicate the subgenus it belongs to. But since the petiole varies so much in this subgenus as well as in the whole genus, these two characters cannot be used in combination as good subgeneric features.

As Emery mentioned in "Genera Insectorum," *Pseudocyrtomyrma* is derived from the small African *viscosa-decemdentata* group of the subgenus *Myrma*. Quite obviously, there has been no clear differentiation between these two subgenera. The evidence is that even when *Pseudocyrtomyrma* was proposed by

Emery, he himself probably did not have a definite idea of this group, because he included Forel's *Polyrhachis spitteleri*, but put Santschi's *P. monista* (fig. 56) under *Myrma*. Actually, these two species differ only in the width of both promesonotal suture and metanotal groove, characters inconstant in these two subgenera. Besides, there is a species from Ivory Coast (figs. 40, 41) with two ridges on the alitrunk. When Emery first erected this subgenus, he mentioned that this subgenus (with type species *P. revoili*, c.f. figs. 54, 55) differs from *Cyrtomyrma* in its much smaller head, and in the propodeum, which has a declivitous face distinct from the basal face (Emery 1921). However, in all aspects, *Pseudocyrtomyrma* is much more closely related to *Myrma* than it is to *Cyrtomyrma*, even if it is to be regarded as a distinct unit in itself.

When Chapman proposed the subgenus *Anoplomyrma*, no diagnostic characters were given for it. But characters can be deduced from the type species *Polyrhachis parabiatica* (figs. 48, 49). The alitrunk has two pronotal spines projecting forward, but has rounded sides and no teeth or tubercles on the propodeum. The petiole is scale-like, although rather thick. The scale-like petiole is not particular at all, as it is also found in *Myrma*. As to the alitrunk, one species (figs. 50, 51) shows obsolescent margins on the alitrunk. Another species (figs. 52, 53) has the alitrunk as smooth as in *Cyrtomyrma*. Furthermore, the male genitalia of this species also shows that it is closely related to *Myrma*.

The subgenus *Hagiomyrma* (figs. 57-62) is characterized by the pronotum, which usually has shoulders laminate but not armed. Propodeal spines long. Petiole usually scale-like, with two spines curved backward, or downward, or simply raised upward. In some species, the node is thick and with flat or sloped dorsum. However, the unarmed pronotum and long propodeal spines can be derived from *Campomyrma*. Furthermore, in some species, such as *P. sokolova* (fig. 62), the pronotum is armed with angular laminae, and not much difference exists between this species and *P. semipolita* of the subgenus *Campomyrma*.

"Pronotum convex and petiole high, flattened above, with two horizontal diverging spines" are the characters used to separate subgenus *Hedomyrma* from others. However, the convexity of

pronotum forms a gradual morphocline from some *Hagiomyrma* to *Hedomyrma*. A flat-topped petiole is also found in *P. thusnelda* of *Hagiomyrma*. Furthermore, in *P. kershawi* of *Hedomyrma* (figs. 64, 65), the petiole actually does not have a flat top, but slopes. *P. (Dolichorhachis) malaensis* (fig. 68) and *P. (Hagiomyrma) terpsichore* (fig. 69) are quite similar; the main difference to be considered is the metanotal groove, distinct in the former, but rather effaced in the latter, as in most *Hedomyrma*.

In some *Chariomyrma* (figs. 70-74), the broad, flat humerus, which may sometimes be incised, serves as a notable character. As for the petiole, it does not differ much from that of *Hagiomyrma*. But there are also forms such as *P. arcuata*, in which the pronotum looks very much like that of *Hagiomyrma*. Sometimes the hairy body is used as a character, but *P. (Chariomyrma) urania* is not so hairy, and some *Hagiomyrma* are quite hairy, too.

If only the type species *P. porcata* is concerned, *Aulacomyrma* is characterized by the strong ridge on the first gastric tergite (fig. 75). But this ridge is reduced in other species of this subgenus, as may be seen in *P. mystica*. This group is closely related to *Chariomyrma* so far as the alitrunk is concerned. But no ridge or groove to receive the petiole is found on the gaster in *Chariomyrma*. *P. jerdoni* (fig. 79) of *Myrmhopla* has margined alitrunk and a ridge on the gaster, thus serving to link *Aulacomyrma* and *Myrmhopla*.

Cyrtomyrma (figs. 87-93) and *Polyrhachis (sens. str.)* (figs. 94-99) are rather unusual in this genus. In *Cyrtomyrma*, the following characters need consideration:

1. Head with gena distinctly separated from postgena by occipital suture which forms a ridge. Postgena flat.
2. *P. levior* with naked pupae (Wheeler 1915b).
3. Workers of *P. levior* and *P. townsvillei* with three ocelli (Donisthorpe 1938).

Some species such as *linae* (fig. 87) and *doddi* (fig. 88) look very much like some *Myrmhopla*, but the three above characters are not found in *Myrmhopla*. In *Polyrhachis (sens. str.)*, the follow-

ing hold:

1. It has both pro- and mesonotal spines (this combination is not found in other groups).
2. Petiole columnar, surmounted by two long spines (this kind of petiole is found only in *furcata* of *Myrmhopla*, but here the rest of the characters differ widely).
3. A median ocellus is found in the workers of the *ypsilon* complex and becomes obscure in *bihamata* and *bellicosa*.
4. In other groups, the petiole of females often looks much like that of workers both in length and shape. But in this group, it is very much reduced in length and shape.

From the discussion above, we come to the conclusion that all the subgenera in this genus except perhaps *Cyrtomyrma* and *Polyrhachis* (*sens. str.*) are so intergradient with one another that a clear delimitation is not found between any two related groups. Subgenus *Polyrhachis* may be a good genus by itself, but this assumption needs further investigation.

THE NESTS OF POLYRHACHIS

Polyrhachis has very diverse nesting habits. Ants of some subgenera nest in the soil, others in the ground under stones, logs, etc. Some nest in rotten logs, hollow stems, or any suitable plant cavity. Still others build their nests of silk or carton on or among leaves of plants. But there are several subgenera that build nests both under and on the ground surface.

Ants of the subgenus *Cyrtomyrma* build, almost without exception, silken nests attached to the leaves of trees. They are dominants among the *Polyrhachis* subgenera in the high arboreal zone and have greatly reduced spines. *Myrmhopla* species nest and forage almost exclusively in the lower arboreal zone. They usually build globular carton nests in low bushes among leaves and twigs. But sometimes they may nest in the hollow joints of bamboos, or even in houses. In China, *P. dives* is occasionally found nesting underground in tree bases and hedgerows (Brown, pers. commun.), and in India and Asia Minor, *P. simplex* weaves a unilocular nest of larval silk underground. Little is known about the nest in the subgenus *Aulacomyrma*. The only species for

which the nest is described is *P. mystica* (Karawajew 1928), which builds carton nests on leaves of trees. In *Myrmatopa* and *Myrmothrinax*, carton nests are constructed on or under leaves.

The subgenus *Polyrhachis* contains mostly arboreal-nesting species. However, *lamellidens* is usually found nesting in rotten logs or tree cavities (Yano 1911), but occasionally nests underground (Brown, pers. commun.), and *erosispina* nests in herbaceous and shrubby ground vegetation (Wilson 1959). The East Indian *bihamata* builds its nest of silky yellowish-brown material, placed close to the ground in the center of a clump of bamboos (Bingham 1903). *P. annae* is the only species in the subgenus *Hedomyrma* of which the nest has been described. It was found in earth among the suckers of an epiphyte (Mann 1919). Mann added that the colonies usually nest high in trees. Whether silk is employed in the construction of the nest is not reported.

Myrma has the most diverse nesting habits of all the subgenera. A nest of *P. laboriosa* was found in a fork of a bush in a cluster of fine twigs (Wheeler 1922). It consists of coarse vegetable particles bound together by a small quantity of silk. No soil enter into its construction. A nest of *P. bequaerti* consisting of two leaves united by a soft tissue of fibrous, gnawed vegetable particles and silk was described from Africa by Wheeler (1922). *P. otleti* nests in crevices of bark covered with silk mixed with vegetable material (Forel 1916). Forel also described a nest of *P. monista* which was found in a rolled leaf (Forel 1916a). This species is very closely related to *P. spitteleri* (c.f. discussion in previous section). A chimney nest attached to the lower surface of a leaf is built by *P. alluaudi* in Africa (Emery 1891). Nests of some other *Myrma* are found in crevices of trees, in hollow fern-stalks, in rotten logs, or on the ground under logs or other objects, and some species use silk to make partitions or protecting walls. *P. gagates* (Wheeler 1922) and *P. schistacea divina* (Weber 1943) nest in the ground, and a certain amount of silk is employed. A nest of *P. (Anoplomyrma) parabiatica* has been found in a dead frond of a tree fern (Chapman 1963). Perhaps silk is also used to tie the frond together.

Species of *Campomyrma* usually nest in the ground, under stones, or more rarely in crater nests. So do species of *Chario-*

myrma and *Hagiomyrma*, although *P. (Hagiomyrma) semiaurata* has been found in large logs, and certain species of *Chariomyrma* nest in earthen termitaria (Wheeler 1922). So far as is known, no silk is employed in the construction of nests in these three subgenera, except for *P. (Campomyrma) halidayi*, which makes comparatively large nests among the leaves of trees (Bingham 1903), and *P. (Campomyrma) patiens* which nests under stones with silk (Brown, pers. commun.).

To sum up, four types of nests of the genus *Polyrhachis* may be recognized, namely:

1. Arboreal: carton and silk nests among leaves and twigs.
2. Lignicolous: nests in the cavities of plants.
3. Terrestrial: nests on the ground under any objects.
4. Subterranean: nests in the soil, without cover.

However, because of the overlapping of some subgenera (for instance, all types are found in *Myrma*), and several exceptions within a single subgenus, it is rather difficult to assign any subgenus to a particular type. But one thing to be noted is that the nesting behavior seems to be somewhat correlated with the shape of the alitrunk and the geographical distribution of the groups. In most cases, those that have rounded alitrunk tend to have arboreal types of nests (except *Myrmotherinx*). The absence of cocoons in *P. (Cyrtomyrma) laevior* (Wheeler 1915b) may be an adaption to this type of nest. The assumption in this genus is that, as habitats move from underground up to the trees, there arises a selective pressure against the margins on the alitrunk. This is well illustrated by *Myrma*, which has the widest range of distribution in this genus. In Asia and New Guinea, *Myrma* species apparently never build arboreal nests. But in Africa, where only *Myrma* and *Pseudocyrtomyrma* exist, four types of nests are found. *Pseudocyrtomyrma* in Africa, and *Anoplomyrma* in the Philippines, both closely related to *Myrma*, have the alitrunk rounded and build arboreal nests.

TENTATIVE PHYLETIC SCHEME

In the previous section, we assumed that subgenus *Campomyrma* is the most primitive group in this genus. This assumption and the

relationships of the groups are outlined in fig. 102. The assumption is supported not only by the morphological character of the alitrunk, but also by the nesting behavior and the shape of the acidopore.

As shown in the dendrogram, four main branches radiate from *Campomyrma*, in which the acidopore is formed partly in the hypopygium and partly in its phragma, and has a fringe of hairs. This group also has the most primitive form of nest, either subterranean or terrestrial. *Myrmotherinx* has lost the fringe of hairs and has an arboreal nest. *Myrmatopa* also has an arboreal nest, but the acidopore is more advanced, with the opening entirely in the phragma. *Hagiomyrma*, *Hedomyrma* and *Chariomyrma* still have terrestrial nests, but the acidopore is more derivative, with hairs present only on the hypopygium. From *Aulacomyrma* up to *Cyrtomyrma*, the opening is finally formed entirely in the phragma, and the tip of the hypopygium is shield-like with tufts of hairs on each side. The nest is almost entirely arboreal, with a few exceptions in *Myrmhopla*.

Myrma represents another branch which, probably due to its wide range of distribution, has all types of nests. In Asia, it leads to *Anoplomyrma* and *Polyrhachis* (*sens. str.*), although this lineage is still in doubt. In Africa, it leads to *Pseudocyrtomyrma*. This branch has another type of acidopore, which is formed entirely in the phragma, and the tip of the hypopygium is rounded along its sides.

To sum up, the groups on both sides of the dendrogram tend to evolve a rounded alitrunk and an arboreal type of nest, and the acidopore also tends to be formed entirely in the phragma.

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EXPLANATION OF FIGURES

- Figs. 1-97. Alitrunks and petioles, usually both, and occasionally heads and gasters of the named species.
- Figs. 98-100. Male genitalia of the named species.
- Fig. 101. Photograph of a syntype worker of *kirkae*.
- Fig. 102. Tentative phyletic scheme. Groups which may be related phyletically are joined by lines but the length of these lines does not indicate the degree of the relationships. The dotted line indicates an uncertain relationship.

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clypeata



schwiedlandi



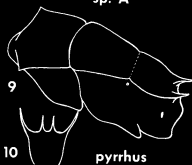
prometheus



sp. A



halidayi



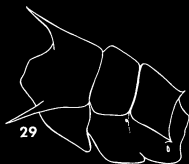
pyrrhus

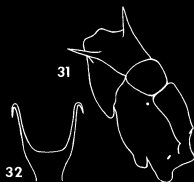


semipolita



sidnica

**frauenfeldi****unicuspis****thrinax****solivaga****wallacei****schang****edwardi****lombokensis****militaris**



laboriosa



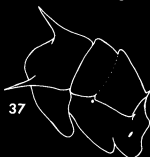
rufofemorata var.
semirufofemorata



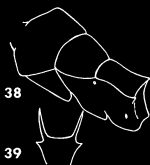
cubaensis var. *gallicola*



fissus



mayri



sp. B



sp. C



viscosa

**philippinensis**

46

orsyllus

47

decemdentata

48



49

parabiotica

50



51

sp. D

52



53

sp. E

56

monista

54



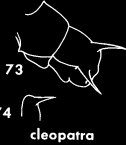
55

revoili

57

58

ammon





75

porcata

76



77



78

mystica

79

jerdoni

80

schizospina

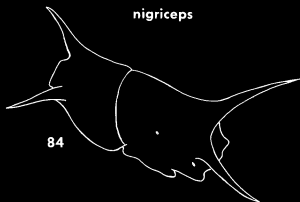
81

stylifera

82



83

nigriceps

84

armata



hippomanes

linnae

doddi



gibba

doddi

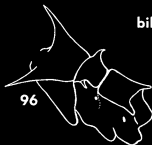
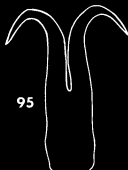
linnae

laevissima

demangei

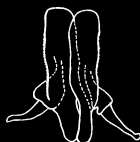


bihamata



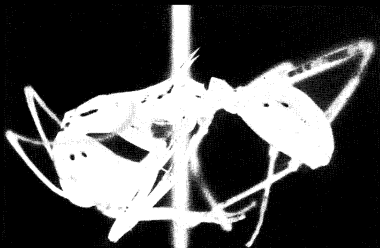
lamellidens



*osae**laboriosa*

100

*mucronata*



101

